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Facial Width-to-Height Ratio is Associated with  
Agonistic and Affiliative Dominance in Bonobos (*Pan paniscus*)

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**Abstract**

Facial width-to-height ratio (fWHR) is associated with social dominance in human and non-human primates, which may reflect the effects of testosterone on facial morphology and behavior. Given that testosterone facilitates status-seeking motivation, the association between fWHR and behavior should be contingent on the relative costs and benefits of particular dominance strategies across species and socioecological contexts. We tested this hypothesis in bonobos (*Pan paniscus*), who exhibit female dominance and rely on both affiliation and aggression to achieve status. We measured fWHR from facial photographs, affiliative dominance with Assertiveness personality scores, and agonistic dominance with behavioral data. Consistent with our hypothesis, agonistic and affiliative dominance predicted fWHR in both sexes independent of age and body weight, supporting the role of status-seeking motivation in producing the link between fWHR and socioecologically relevant dominance behavior across primates.

**Keywords:** fWHR, dominance, motivation, personality, bonobo, socioecology

## Introduction

Androgens play a key role in sexual differentiation and the promotion of competitive social behavior across vertebrates [1]. While short-term changes in testosterone can activate the expression of dominance behavior, androgen exposure during key developmental windows can also induce long-term organizational effects on the adult phenotype [2]. These organizational androgen effects (OAE) can cause consistent individual differences in behavior (i.e. personality; e.g., [3]) and other androgen-sensitive phenotypes such as facial morphology [4] and digit ratios [5]. Much effort has been put into validating potential biomarkers of OAE, which may proxy prenatal and/or pubertal androgen exposure [6] and act as sexually selected signals in intra-sexual competition and mate choice [7]. The facial width-to-height ratio (fWHR), which compares the bizygomatic breadth to the distance between the brow ridge and upper lip (see figure 1), has been proposed as one such OAE biomarker [8]. fWHR predicts social dominance behavior across multiple contexts [9,10,11; but see 12,13] and species (*Macaca spp.* [14]; *Sapajus spp.* [15,16]), exhibits a small degree of male-biased sexual dimorphism [9,17], and associates with other proposed OAE biomarkers such as the 2<sup>nd</sup>-to-4<sup>th</sup> digit ratio (2D:4D; [18]).



**Figure 1.** Facial-width-to-height ratio.

*Footnote.* fWHR was measured by dividing the bizygomatic breadth (white box width) by the distance between the brow ridge and upper lip (white box height). The tragus was used for reference when facial hair covered the maximal cheek prominence.

While it has long been recognized that testosterone facilitates agonistic behavior, recent work has shown that testosterone enhances status-seeking motivation and thus social dominance behavior more generally [1,19]. Contingent upon the social context, dominance behavior can manifest in diverse ways ranging from intimidation and aggression to gregariousness and prosocial leadership [20]. The association between fWHR and behavior is therefore expected to reflect the relative costs and benefits of particular dominance strategies in the species and socioecology under investigation. Consistent with this hypothesis, higher fWHR has been found to predict aggression in low-status men [21], but also prosocial leadership in high-status men [10]. Moreover, as expected given the higher costs of physical aggression for human females, fWHR in females is associated with self-reported dominance and verbal aggression but not with physical aggression [9,22].

Bonobos (*Pan paniscus*) provide a valuable system for further examining the relationship between fWHR and dominance behavior in a novel socioecological context. As is typical for humans and mammals more generally, male bonobos experience greater exposure to testosterone during sexual maturation [23]. fWHR should therefore be larger in male bonobos if this trait is an OAE biomarker. In contrast to most human societies, however, female bonobos often exhibit social dominance over males [24,25]. Moreover, while both males and females use agonistic behavior during competitive encounters, they also rely heavily on affiliation and coalitionary support to achieve social status [24,26,27].

Previous work in captive bonobos has demonstrated that individuals rated as being more dominant, confident, and calm—thus exhibiting a higher degree of the personality dimension Assertiveness [28]—tend to receive more allogrooming, have a higher number of conspecifics in close proximity, get approached more often, and receive less aggression [29]. In contrast to the personality dimension Assertiveness in brown capuchins (*Sapajus spp.*), however, which has previously been found to predict fWHR [15,16], Assertiveness in bonobos reflects affiliative dominance rather than aggressiveness or agonistic dominance. Consistent with the importance of coalitionary support for female dominance in bonobos [30], female bonobos score higher in this dimension than males [29]. Bonobo Assertiveness therefore more closely aligns with the social assertiveness aspect of Extraversion in humans, which reflects a motivation toward achieving prestigious and affiliative forms of social dominance such as leadership [31]. If testosterone exposure influences facial morphology and status-seeking motivation in bonobos, fWHR should therefore be positively associated with both agonistic and affiliative dominance behavior across males and females. In the present study, we integrate behavioral, morphometric, and psychometric data to test this hypothesis.

## Materials and Methods

### *Subjects and Measures*

All data were collected from 2011 to 2014 on 38 sexually mature bonobos (15 males, 23 females; age range: 10-62 years, mean = 23.87 years, SD = 11.91 years) housed in five European zoos as part of a larger project on personality in bonobos [28,29].

96 *fWHR*

97         NS collected facial photographs taken ad libitum while the bonobos were on exhibit. She  
98 attempted to capture front-facing portraits for each individual while they were exhibiting a neutral  
99 expression with their mouth closed, and we discarded photos in which individuals covered their  
100 face and/or exhibited non-neutral facial expressions. This resulted in a total of 117 photographs,  
101 with an average of 3 acceptable images per individual. JSM measured fWHR from these photos as  
102 the bizygomatic breadth divided by the distance between the brow ridge and upper lip (see figure  
103 1), which was subsequently standardized by the inter-pupil distance to adjust for heterogeneous  
104 scaling across photographs [32]. All measurements were made using Adobe Photoshop CC. A  
105 trained research assistant blind to our hypotheses independently measured fWHR in a randomly  
106 selected sample of 25% of our photographs, demonstrating appropriate single measurement  
107 reliability for fWHR as assessed by the intra-class correlation coefficient,  $ICC(3, 1) = 0.78$ .

108 *Affiliative dominance*

109         We assessed affiliative dominance using Assertiveness scores derived from the Hominoid  
110 Personality Questionnaire [28], which was administered to multiple human raters with extensive  
111 experience observing the bonobos. Individuals scoring high on Assertiveness were rated as being  
112 higher on traits such as *independent*, *dominant*, *decisive*, and *persistent*, as well as lower on traits  
113 like *submissive*, *anxious*, *vulnerable*, and *fearful*. The ratings of bonobo Assertiveness used in the  
114 present study exhibited appropriate inter-rater reliability and repeatability and were found to  
115 predict relevant behavioral measures of affiliative dominance [29].

116

117

## 118 *Agonistic dominance*

119         We used normalized David's scores (DS) [25] as a measure of individual differences in  
120 agonistic dominance [29]. Individuals with higher DS elicited a higher proportion of fleeing  
121 behavior from their competitors during agonistic encounters. We mean-centred DS within each  
122 zoo to adjust for differences in the opportunity for agonistic encounters, thus facilitating  
123 comparison of relative agonistic dominance across zoos.

## 124 *Statistical Analysis*

125         All statistical analyses were conducted using linear regression models fit and interpreted  
126 within a Bayesian framework. Measurement error models were utilized to account for uncertainty  
127 in the mean fWHR measurement of each subject, and we used regularizing priors,  $\beta \sim \text{Normal}(0,2)$   
128 for fixed effects and  $\sigma \sim \text{Half - Cauchy}(0,2)$  for the residual standard deviation, to penalize  
129 extreme estimates and reduce our risk of inferential errors [33]. Age and sex were included as  
130 covariates in all analyses. We estimated models both excluding and including body weight to  
131 determine whether potential associations between behavior, sex, and fWHR were independent of  
132 body size, as previous research has suggested that the relationship between fWHR and behavior  
133 may be a by-product of the association between body size and facial morphology (e.g., [34]).  
134 Recent body weight measures were only available for a subset of our sample ( $N = 22$ ). We used  
135 Bayesian imputation to estimate the unmeasured body weights for the remaining subjects, thus  
136 avoiding an appreciable loss of information as well as systematic bias in our estimates due to the  
137 incorrect assumption of data missing completely at random (MCAR). In addition to our full main  
138 effects model, we also assessed whether sex interaction effects were present for affiliative or  
139 agonistic dominance. For comparison with [15], we further estimated a model including an  
140 interaction between affiliative and agonistic dominance.

Rather than relying on null hypothesis tests, we based our inferences on the information provided by standardized regression coefficients ( $\beta$ ), the median absolute deviation (MAD) as a robust estimate of dispersion, the 90% credible interval (CI), and the posterior probability of observing an effect in the direction of the median (i.e.,  $p_{>0}$  or  $p_{<0}$ ). In addition, we report Cohen's  $f^2$  for our fixed effects, which provides a standardized measure of local effect size for multiple regression. Values of  $f^2 \geq 0.02$ ,  $f^2 \geq 0.15$ , and  $f^2 \geq 0.35$  are traditionally interpreted as small, medium, and large effects, respectively [35]. Tildes are used throughout to denote posterior median estimates of these values. fWHR measures were standardized to z-scores, and all non-binary covariates were standardized to 2\*SD variance to facilitate comparison with the binary sex effect. Please see the electronic supplementary material for further details on our statistical analyses.

## Results

Male bonobos exhibited larger fWHR than females ( $\tilde{\beta} = 0.43$  [MAD = 0.26], 90% CI [0.01, 0.89],  $p_{>0} = 0.95$ ,  $\tilde{f}^2 = 0.07$ ). The effect of sex was reduced, however, after controlling for body weight ( $\tilde{\beta} = 0.25$  [0.22], 90% CI [-0.13, 0.62],  $p_{>0} = 0.87$ ,  $\tilde{f}^2 = 0.10$ ), while body weight exhibited an independent positive association with fWHR ( $\tilde{\beta} = 0.87$  [0.18], 90% CI [0.59, 1.20],  $p_{>0} = 1$ ,  $\tilde{f}^2 = 0.83$ ; see figure 2A). Controlling for body weight, age, and sex, fWHR was positively associated with both affiliative ( $\tilde{\beta} = 0.83$  [0.18], 90% CI [0.52, 1.12],  $p_{>0} = 1$ ,  $\tilde{f}^2 = 0.54$ ; see figure 2B) and agonistic dominance ( $\tilde{\beta} = 0.43$  [0.21], 90% CI [0.08, 0.77],  $p_{>0} = 0.98$ ,  $\tilde{f}^2 = 0.13$ ; see figure 2C). There was a negative effect of age on fWHR ( $\tilde{\beta} = -0.54$  [0.24], 90% CI [-0.93, -0.16],  $p_{<0} = 0.99$ ,  $\tilde{f}^2 = 0.35$ ). Little evidence was found for sex-specific links between fWHR and affiliative ( $\tilde{\beta} = -0.01$  [0.40], 90% CI [-0.67, 0.64],  $p_{<0} = 0.51$ ,  $\tilde{f}^2 = 0$ ) or agonistic dominance ( $\tilde{\beta} = -0.29$  [0.43], 90% CI [-1.01, 0.41],  $p_{<0} = 0.75$ ,  $\tilde{f}^2 = 0.01$ ), and agonistic and affiliative dominance did not exhibit

an interaction effect on fWHR ( $\tilde{\beta} = 0.11$  [0.45], 90% CI [-0.62, 0.88],  $p_{>0} = 0.61$ ,  $\tilde{f}^2 = 0$ ). Overall, our main effects model accounted for a large proportion of the observed variance in fWHR ( $\tilde{R}^2 = 0.63$ ).

**Figure 2.** fWHR, sex, and social dominance in bonobos.

*Footnote.* Main effect model estimates (predicted median and 90% CI) for the association of male (blue) and female (green) fWHR with (A) body weight, (B) affiliative dominance and (C) agonistic dominance, conditional on average covariate values. Continuous predictors were standardized to 2 SD and are therefore displayed in the [-0.5, 0.5] interval for comparison with a 1 SD change in fWHR.

## Discussion

We found that fWHR was associated with the expression of socioecologically relevant dominance behavior in male and female bonobos. These findings were independent of body weight, suggesting that fWHR provides unique information about personality and dominance beyond body size (cf. [32]). While fWHR has been linked to variation in agonistic dominance styles across macaque species [14], the present study is the first to demonstrate that fWHR also predicts intraspecific variation in affiliative dominance in a non-human primate. This provides a crucial link to human research demonstrating positive associations between fWHR and prosocial behavior in high status contexts [10]. Indeed, the stronger association between affiliative dominance and fWHR (Cohen's  $\tilde{f}^2 = 0.54$ ) compared to agonistic dominance ( $\tilde{f}^2 = 0.13$ ) is consistent with the greater importance of coalitionary support and affiliation in bonobo societies [24,26,27], and thus the role of testosterone for promoting socioecologically relevant status-seeking behaviour rather than aggression per se [1,19]. The observed male-bias in fWHR also provides indirect support for the role of testosterone in producing the association between fWHR

and affiliative dominance, as males experience greater increases in pubertal testosterone than females [23]. Nonetheless, this sex difference was reduced after controlling for body weight, which positively predicted fWHR, suggesting that the observed sexual dimorphism in bonobo fWHR reflects allometric scaling with body size. Testosterone also influences body size [36], however, and may therefore be a common cause of this association.

We also observed a negative association between age and fWHR, consistent with previous research demonstrating declining fWHR in human populations across the lifespan [37]. Dominance ranks have been observed to vary within bonobo and chimpanzee societies across time in sex-specific ways, with critical factors such as personality, competitive ability, and social support exhibiting sex- and age-specific influences on social status [e.g., 38,37,40]. Given the cross-sectional nature of our study design, it remains unclear whether the observed age- and sex-independent associations between fWHR and social dominance are consistent across ontogeny. However, our data do not provide any clear support for interaction effects between sex, age, and/or social dominance on fWHR (see electronic supplementary material for further analyses). These results tentatively suggest that the organizational effects of testosterone on status-seeking motivation may also stabilize associations between fWHR and observed dominance across the lifespan. Nevertheless, future longitudinal research with greater statistical power will be crucial for examining these developmental patterns.

Relatedly, the validity of fWHR as an OAE marker cannot be directly assessed without an accurate measure of androgen exposure during the critical organizational periods of brain and facial development. The hypothesized connection between fWHR and androgen exposure in humans remains unclear, as recent work has not found strong associations between fWHR and pubertal [32; but see 41] or prenatal [4] testosterone levels or exposure, respectively. Moreover,

fWHR is not strongly associated with polymorphisms in the androgen receptor gene, which also does not moderate the androgen-fWHR association [42]. Nonetheless, aspects of human facial width have been found to reflect prenatal testosterone [4] and exhibit male-biased sexual dimorphism across the lifespan [43]. This suggests that more complex experimental designs will be needed to disentangle the causal bases of the facial components underlying composite measures such as fWHR [44]. Investigating the mechanisms linking fWHR and behavior is therefore an important task for future research. Given that organizational effects are hypothesized to cause the association between fWHR and behavior, studies of baseline testosterone levels or activational effects in adults may not clarify this issue [cf., 45].

In sum, our study demonstrates that fWHR is linked to both agonistic and affiliative forms of social dominance in a non-human species. In conjunction with previous work linking fWHR and social dominance behaviour in humans [9,10], macaques [14], and capuchins [15,16], our findings suggest that facial morphology may provide reliable cues of status-seeking motivation and testosterone exposure prior to sexual maturity. Identifying whether non-human primates use this information for social decision-making is thus a clear target for future research. For example, female rhesus macaques (*Macaca mulatta*) have been demonstrated to perceive differences in male facial masculinity [46], suggesting that fWHR may be a signal of intra-sexual competitive ability used in partner choice. Given that female bonobos often exhibit social dominance over males [24,25], it would be valuable to examine whether male bonobos can also perceive dominance information encoded in female faces. In addition, understanding the sociocognitive effects of facial morphology in the context of varying facial hair and coloration also remains important for determining the ecological relevance of such discriminations [47]. Irrespective of their communicative function, however, consistent associations have now been identified between



fWHR, dominance rank, and status-seeking motivation in humans, bonobos, and capuchins. The organizational effects of testosterone may therefore be an important and phylogenetically conserved mechanism of personality across haplorrhine primates.

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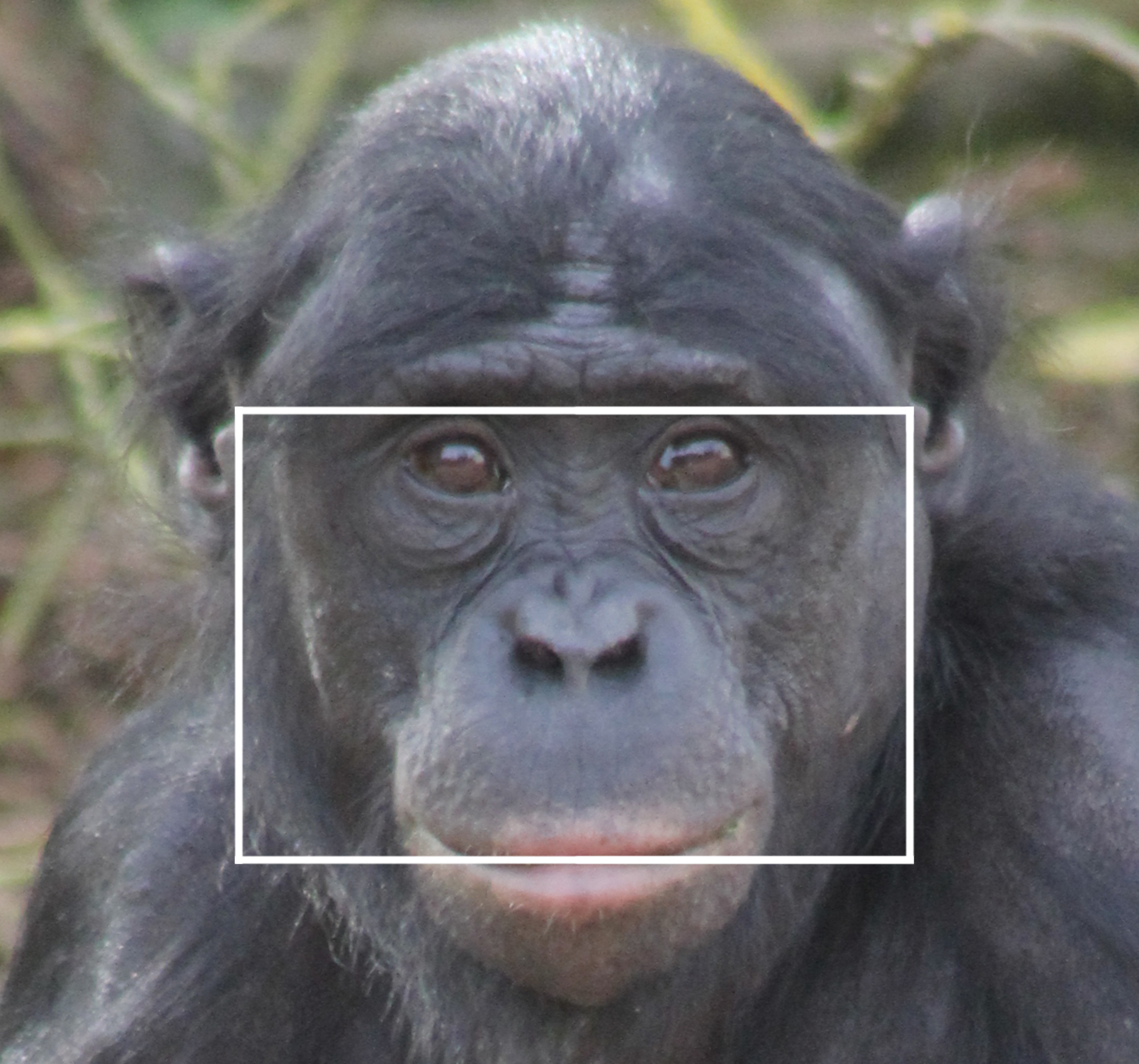
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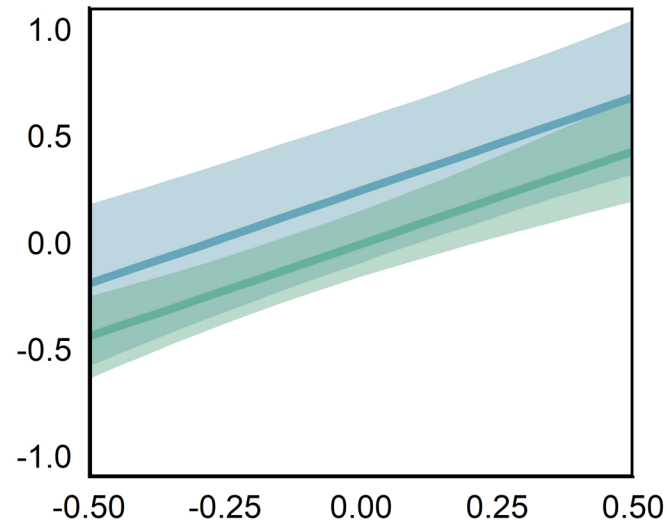
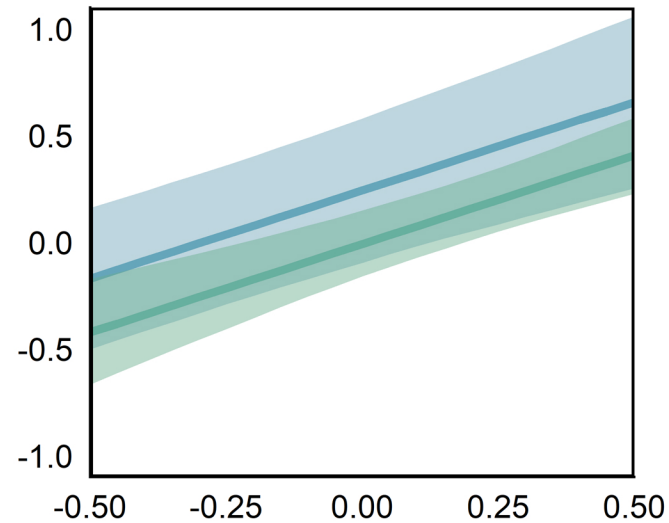
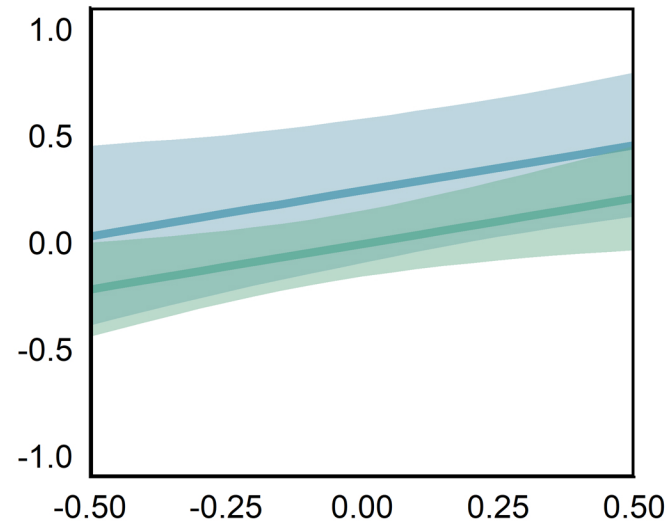
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**A****B****C**

## Supplementary Information for

### Facial Width-to-Height Ratio is Associated with Agonistic and Affiliative Dominance in Bonobos (*Pan paniscus*)

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## Supplementary Methods and Results

### *Subjects and measures*

A random sampling procedure was used to reduced researcher bias during facial measurement. NS removed identifiable information from photographs and randomly selected a subset of subjects from each zoo with available facial photographs, which were subsequently measured by JSM and a research assistant, neither of whom took part in collection of the behavioral and psychometric data. As described in the main text, appropriate photos with neutral expressions and forward-facing orientation were subsequently selected and measured for these subjects. fWHRs were then paired back with the remaining individual data after these measurements were completed.

Organizational effects of androgen exposure on behavior and facial morphology could plausibly occur from the prenatal period until sexual maturity. We therefore sought to focus our analysis on sexually mature bonobos. Previous research on captive bonobos suggests that the onset of puberty is likely to occur from approximately 6-10 years of age, with the sharpest increase in urinary testosterone around 8-9 years of age for males and an earlier but more gradual increase in females [1]. We therefore excluded three 7 year old subjects from our final dataset who we could not confidently classify as sexually mature. This resulted in a final sample of 38 individuals across five social groups. Demographic data on the resultant sample is provided below (**Table S1**).

**Table S1.** Sample demographics.

Zoo	<i>n</i>	# Males	# Females	Average age (range)
Apenheul	5	2	3	19.6 (13-34)
Frankfurt	7	2	5	25.6 (11-62)
Planckendael	5	3	2	17.4 (10-27)
Twycross	8	3	5	22 (10-36)
Wilhelma	7	2	5	28.1 (11-48)
Wuppertal	6	3	3	28.3 (12-49)

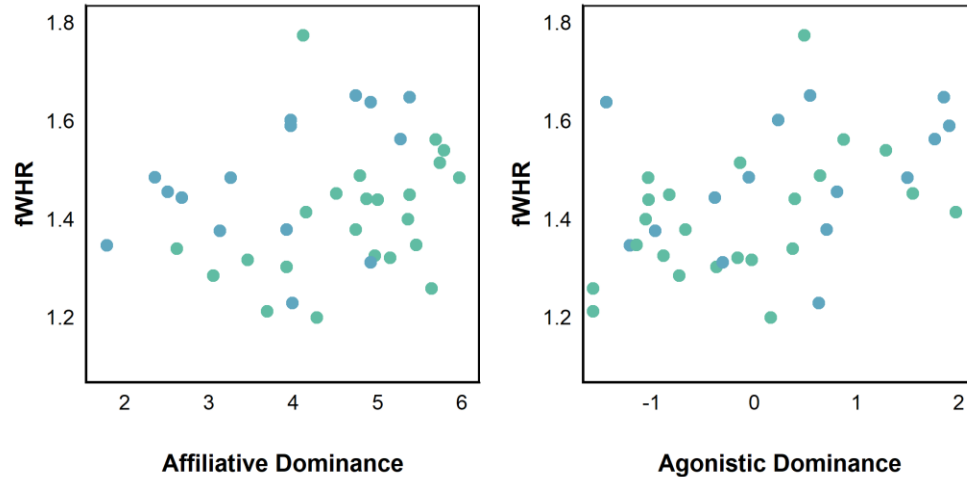
*Footnote.* Age in listed in years.

In the 22 subjects with available body weight measures, moderate to strong associations were also observed between sex and weight ( $r_{\text{Biserial}} = 0.82$ ) and fWHR and weight ( $r = 0.36$ ). In our full sample, fWHR and sex exhibit a similarly sized association ( $r_{\text{Biserial}} = 0.36$ ). While the relationship between sex and fWHR may be mediated by body weight, as suggested by our primary regression model (**M1**; see below), testosterone is also a known cause of individual differences in body size [2]. It therefore remains unclear whether organizational androgen effects may be a latent common cause of these associations. The statistically uncertain sex effect reported in the main text, after conditioning on body weight, should therefore be cautiously interpreted.

Scatterplots of our raw data provide initial support for the association between fWHR and both affiliative and agonistic dominance (**Fig S1**), but also suggest that the strength of affiliative dominance in particular is enhanced by controlling for sex, age and body weight. Consistent with

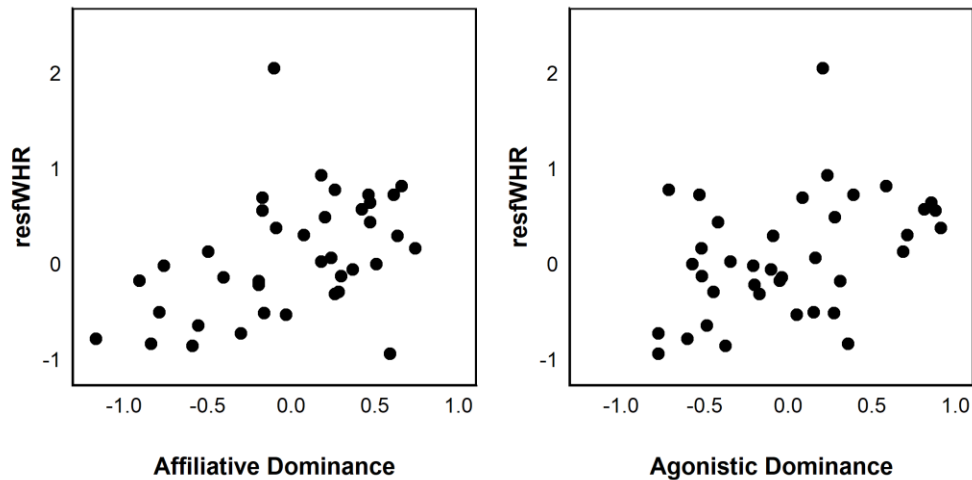
this interpretation, a clearer affiliative dominance association is observed with fWHR residuals after controlling for these factors (**Fig S2**).

**Fig S1.** Scatterplots of fWHR and the social dominance measures.



*Footnote.* Datapoints are colored separately for females (green) and males (blue). Social dominance measures are shown on the original data scale.

**Fig S2.** Scatterplots of fWHR residuals and the social dominance measures.



*Footnote.* Social dominance measures are standardized to 2 SD. resfWHR = residual fWHR controlling for age, sex, and body weight.

It is important to emphasize that our agonistic dominance measure was analyzed using within-group deviations rather than absolute scores. By centering individual scores within zoos, we effectively accounted for differential opportunities for agonistic encounters across zoos. This is necessary because the raw David's scores used as a measure of agonistic dominance are contingent

upon the sample size within each zoo. As further described below, we did not find support for further zoo-specific effects in a random slopes model (**M11** below).

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### Statistical Analysis

We estimated Bayesian linear measurement error models for all analyses using the R package ‘brms’ [3], which interfaces with the Stan statistical programming language [4]. As noted in the main text, we employed a fully Bayesian approach to statistical estimation and inference. Therefore, rather than relying upon null hypothesis tests and arbitrary designations of statistical significance, we used multiple sources of information to summarize and draw inferences from our posterior model estimates [5]. The R Code and dataset for this manuscript have been provided as additional supplementary material and can be used to replicate all analyses described below.

We examined the association between fWHR and measures of affiliative and agonistic dominance, while accounting for error in the measurement of fWHR across photos. In addition to these covariates, we also included fixed effects for years of age and sex in all models. We found that inclusion of random zoo-specific intercepts did not account for a meaningful degree of variance in fWHR ( $\tilde{\sigma}^2 = 0.03$  [MAD = 0.04]) and reduced the efficiency of MCMC model convergence. We therefore excluded this term from our statistical models.

Our first model (**M0**) excluded information on body weight to assess potential sexual dimorphism in fWHR irrespective of body size. We therefore estimated the following formal model structure conditional on the average fWHR measurement for subject  $i$  using Hamiltonian Markov Chain Monte Carlo.

**Model 0 (M0).** Main effects without body weight covariate.

$$\text{fWHR}_{\text{EST},i} \sim \text{Normal}(\mu_i, \sigma)$$

$$\mu_i = \alpha + \beta_{\text{AssR}} + \beta_{\text{wgDS}} + \beta_{\text{Age}} + \beta_{\text{Sex}}$$

$$\text{fWHR}_{\text{OBS},i} \sim \text{Normal}(\text{fWHR}_{\text{EST},i}, \text{fWHR}_{\text{SD},i})$$

$$\alpha, \beta \sim \text{Normal}(0, 2)$$

$$\sigma \sim \text{Half - Cauchy}(0, 2)$$

Here, the expected subject-specific fWHR  $\mu_i$  is represented as a function of the population-level intercept  $\alpha$  and population-level/fixed effects  $\beta$  for Assertiveness scores of affiliative dominance (AssR), within-group David’s scores of agonistic dominance (wgDS), age, and sex. We account for measurement error in fWHR measurements by parameterizing observed fWHR measurements  $\text{fWHR}_{\text{OBS},i}$  as arising from a normal distribution characterized by unknown mean parameter  $\text{fWHR}_{\text{EST},i}$  and the standard deviation  $\text{fWHR}_{\text{SD},i}$  of fWHR measurements for each subject. This structure effectively accounts for uncertainty in our response variable while estimating the

regression parameters, and vice versa [5]. The expected measurement error for subjects with multiple photographs was assigned to 3 subjects with single photographs. Please note that we simplify specification of model priors to represent shared priors over fixed effects ( $\alpha, \beta$ ) and residual and effects ( $\sigma$ ). We also suppress observed covariate values to ease interpretation, so that terms such as  $\beta_{\text{AssR}}$  implicitly denote  $\beta_{\text{AssR} \text{AssR}_i}$ .

For our primary analysis (**M1**), we then included body weight as an additional covariate to assess whether links between fWHR, sex, and social dominance were independent of body size. Recent body weight measures were only available for a subset of our sample, and we therefore used a Bayesian imputation procedure to avoid an appreciable loss of information and statistical power. We used an inclusive predictive model for estimating unmeasured body weights, incorporating all main effect terms in the primary regression model, so as to reduce systematic error and better approximate data missing completely at random (MCAR) [6]. We therefore estimated the following model conditional on our dataset

**Model 1 (M1).** Main effects with body weight covariate.

$$\text{fWHR}_{\text{EST},i} \sim \text{Normal}(\mu_i, \sigma)$$

$$\mu_i = \alpha + \beta_{\text{AssR}} + \beta_{\text{wgDS}} + \beta_{\text{Age}} + \beta_{\text{Sex}} + \beta_{\text{Weight}}$$

$$\text{fWHR}_{\text{OBS},i} \sim \text{Normal}(\text{fWHR}_{\text{EST},i}, \text{fWHR}_{\text{SD},i})$$

$$\text{Weight}_i \sim \text{Normal}(v_i, \sigma_{\text{Weight}})$$

$$v_i = \alpha_{\text{Weight}} + \gamma_{\text{AssR}_v} + \gamma_{\text{wgDS}_v} + \gamma_{\text{Age}_v} + \gamma_{\text{Sex}_v} + \gamma_{\text{fWHR}_v}$$

$$\alpha, \beta, \gamma \sim \text{Normal}(0, 2)$$

$$\sigma \sim \text{Half} - \text{Cauchy}(0, 2)$$

Here, missing values for body weight are imputed using the regression function defined for the subject-specific expectation  $v_i$ , with random predictive uncertainty  $\sigma_{\text{Weight}}$ . Fixed effect terms in this predictive imputation model are noted by  $\gamma$ , rather than the  $\beta$  notation for fixed effects in the main fWHR model, to aid interpretation.

Cohen's  $f^2$  [7] were calculated as suggested by Selya and colleagues [8] to provide a standardized metric of local effect size

$$f^2 = \frac{R_{AB}^2 - R_A^2}{1 - R_{AB}^2}$$

Here  $R_{AB}^2$  is the variance explained by a model containing the parameter of interest B, and  $R_A^2$  is the variance explained by a model of all other parameters A excluding B. An estimated  $f^2$  can be negative as the sampled posterior of  $R_{AB}^2$  may be smaller than  $R_A^2$ . For ease of interpretation, we

report negative values as 0 to denote that no support was found for a relative increase in the explanatory power of the model.

### *Additional interaction effect models.*

For comparison with previous research on capuchins, we also estimated additional interaction models with sex-specific effects for affiliative (**M2**; see R Code for further details) and agonistic dominance (**M3**), as well as an interaction between these dominance measures (**M4**). Given that associations between personality and dominance rank have been found to vary across the lifespan [e.g., 9], we also fit supplementary exploratory models estimating interactions between age and affiliative (**M5**) and agonistic dominance (**M6**), as well as age by sex interactions with affiliative (**M7**) and agonistic dominance (**M8**). No clear interaction effects were observed across models. In addition to the absence of sex-specific interactions reported in the main text, we also did not find support for age interaction effects with affiliative ( $\tilde{\beta} = 0.03$  [0.37], 90% CI [-0.57, 0.66],  $p_{>0} = 0.54$ ,  $\tilde{f}^2 = 0$ ) or agonistic dominance ( $\tilde{\beta} = 0.01$  [0.35], 90% CI [-0.57, 0.58],  $p_{<0} = 0.51$ ,  $\tilde{f}^2 = 0$ ). Sex-specific age interactions were also not present for affiliative ( $\tilde{\beta} = 0.14$  [0.88], 90% CI [-1.28, 1.60],  $p_{>0} = 0.56$ ,  $\tilde{f}^2 = 0$ ) or agonistic dominance ( $\tilde{\beta} = -0.20$  [0.94], 90% CI [-1.75, 1.20],  $p_{>0} = 0.59$ ,  $\tilde{f}^2 = 0$ ).

It is possible that such age by sex interactions for social dominance are non-linear across the lifespan, particularly for male bonobos. We therefore further explored non-linear sex by age interactions for affiliative (**M9**) and agonistic dominance (**M10**) using tensor product smoothing [10]. Given the difficulty of directly interpreting non-linear regression coefficients, we used the Watanabe-Akaike information criterion (WAIC) to conduct a fully Bayesian model comparison [11] between the main effects model (**M1**) and these more complex non-linear interaction models. As with other information criteria such as AIC or BIC, smaller values indicate greater relative model quality and expected predictive validity, such that  $WAIC_{\text{Model A}} - WAIC_{\text{Model B}} \leq -2$  provides minimal support for selection of the more complex Model A. Consistent with the aforementioned results, we found that allowing for non-linear interaction effects did not meaningfully enhance the quality of our models and their expected predictive validity ( $WAIC_{\text{M9}} - WAIC_{\text{M1}} = 4.87$  [SE = 9.33];  $WAIC_{\text{M10}} - WAIC_{\text{M1}} = 5.85$  [SE = 6.47]).

Finally, although we used within-zoo centering on David's scores, thus controlling for differential opportunities for agonistic encounters among zoos, it is possible that other unmeasured zoo-specific effects could still confound our main results. We therefore also estimated a supplementary model (**M11**) examining whether random zoo-specific slopes between social dominance and fWHR enhanced model quality. In support of our main effects model (**M1**), we found that adding parameters for zoo-specific slopes reduced the expected predictive validity of our model ( $WAIC_{\text{M11}} - WAIC_{\text{M1}} = 4.89$  [SE = 2.26]).

Our data therefore do not provide support for more complex relationships between social dominance and fWHR than are described in our main effects model. For these reasons, we relied on **M1** for drawing statistical inferences. Nonetheless, it is important to emphasize that our data provide only modest statistical power for detecting interaction and random slope effects, which would be more effectively examined in larger samples.

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